

中国内蒙古最早始新世的啮齿类¹⁾

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摘要:描述了内蒙古二连盆地伯姆巴期 *Gomphos* 层的啮齿类新材料并命名了一个新属种:周氏原鼠(*Yuanomys zhoui*)。新属种与其他最早始新世的梳趾鼠区别在于颊齿具有纤细且孤立的齿尖和小尖,前尖与后尖横向延伸,面对三角座盆的齿尖面陡直。这些特征在一定程度上与 *alagomyids* 类似。依据古地磁与生物地层对比,这些啮齿类的出现表明,现代类型的啮齿类最早的辐射演化,很可能位于中古新世到最早始新世这个时间段中。

关键词:内蒙古,最早始新世,啮齿类,啮齿类分异时间

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NEW RODENTS FROM THE EARLIEST EOCENE OF NEI MONGOL, CHINA

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Abstract New rodent material is described from the Bumbanian *Gomphos* bed in Earlian Basin, Nei Mongol (Inner Mongolia), China. A new genus and species, *Yuanomys zhoui*, is named. The new species differs from other Early Eocene rodents in having slim and isolated cusps and conules on cheek teeth and transverse paracone and metacone with steep surfaces facing a broad trigon basin. These features of *Y. zhoui* to some degree resemble those of *alagomyids*. Constrained magneto- and biostratigraphically, the occurrence of these rodents indicates that the earliest radiation of rodents with modern aspect probably took place during the period of mid-Paleocene to Early Eocene.

Key words Nei Mongol, Early Eocene, rodents, rodent divergence

1 Introduction

Proximal fossil outgroups to rodents, such as *Sinomylus*, *Heomys*, *Rhombomylus*, *Matutinia*, and *alagomyids* are primarily found in Asia. Outside of Asia, only one species, *Alagomys russelli*, is known from the early Clarkforkian (Cf1), Big Multi Quarry, Washakie Basin, Wyoming, where came as well the earliest known rodent with modern aspect (Dawson and Beard, 1996). The first radiation of rodents with modern aspects in Asia is presumably at the earliest

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Eocene, as represented by several ctenodactyloid rodents from China (Li et al., 1979, 1989; Dawson et al., 1984; Tong and Dawson, 1995) and Mongolia (Shevyreva, 1989; Dashzeveg, 1990a). In terms of dental morphology, alagomyids appear to be the most probable group from which rodents with modern aspect are derived. This is because cheek teeth of alagomyids are low-crowned and cusperate, which show transitional features between the typical tribosphenic tooth pattern common to therian mammals and typical rodent tooth morphology. In contrast, cheek teeth of other potential rodent outgroups are too specialized in having certain degree of unilateral hypsodonty and lophodonty to give rise to the rodent tooth pattern. In addition to their similarity in morphology, alagomyids, including *Alagomys* (Dashzeveg, 1990b; Tong and Dawson, 1995; Dawson and Beard, 1996), *Tribosphenomys* (Meng et al., 1994, 2007b; Meng and Wyss, 2001; Dashzeveg, 2003; Lopatin and Averianov, 2004a, b) and *Neimengomys* (Meng et al., 2007b), also coexist with the earliest rodents temporally and paleogeographically, with the primitive alagomyids, *Tribosphenomys*, predating the earliest rodents in Asia.

Here we report some new ctenodactyloid rodents from the earliest Eocene of Nei Mongol (Inner Mongolia), China. These rodents are represented by fragmentary specimens, but fill a geographic gap for the earliest Eocene rodents of Asia. These specimens present new dental morphology that is informative in understanding the morphological transformation of early Glires from alagomyid-like tooth pattern to typical rodent tooth. The occurrence of these rodents, constrained with magnetostratigraphic sequence, casts new light on the divergence time of rodents.

2 Geological setting

The specimens described here were collected by screenwashing from the upper Nomogen Formation at the Wulanboerhe transect in 2003. The Wulanboerhe is south of the Nuhetingboerhe and north of the Huheboerhe (Meng et al., 2007c). Fig. 1 is a composed section of the region based on Meng et al. (2007c) and Sun et al. (2009). Matrices screenwashed have been taken from strata below and above the beds that produce the rodent specimens described here (Fig. 1). The lower part of the Nomogen Formation yields a typical Late Paleocene (Gashatan) fauna, characterized by the presence of *Lambdopsalis*, *Prionessus* and *Palaeostylops*. Three alagomyids, including *Tribosphenomys minutus*, *Tribosphenomys* cf. *T. secundus*, and *Neimengomys qii*, have been reported from this fauna and are collected from several localities of the region (Meng et al., 1998, 2007b; Fig. 1). Species coeval with the new rodents from the same stratum include *Gomphos elkema* (Meng et al., 2004) and a euprimate (Ni et al., 2007; Fig. 1). The *Gomphos* assemblage has been correlated with the Bumbanian land mammal age of Asia (Meng et al., 2004, 2007c; Bowen et al., 2005), and a recent paleomagnetic study places the *Gomphos* bed within chron C24r, presumably at or near the Paleocene–Eocene boundary with the age of 55.8 Ma (Sun et al., 2009). At roughly the same horizon where the *Gomphos* came from exist a species of perissodactyl similar to *Pataecops parvus* and an arctostylopid, *Anatolostylops zhaili*, which is significantly larger than *Palaeostylops macrodon* (Wang et al., 2008). Several fossiliferous levels above the *Gomphos* beds have been discovered but will not be discussed in the present study. These fossil levels, however, provide the biostratigraphic context for interpreting the significance of the new rodents.

3 Methods

For taxonomy, we only use Ctenodactyloidea as the superfamily level taxon, knowing that the family level classification of early ctenodactyloids remains unresolved. Specimens are measured using an Ultra-Cal Mark III digital caliper. Photographs were taken from casts with monotone gray using a Nikon-SZ CCD digital camera mounted to a Nikon SZ-1000 microscope. The

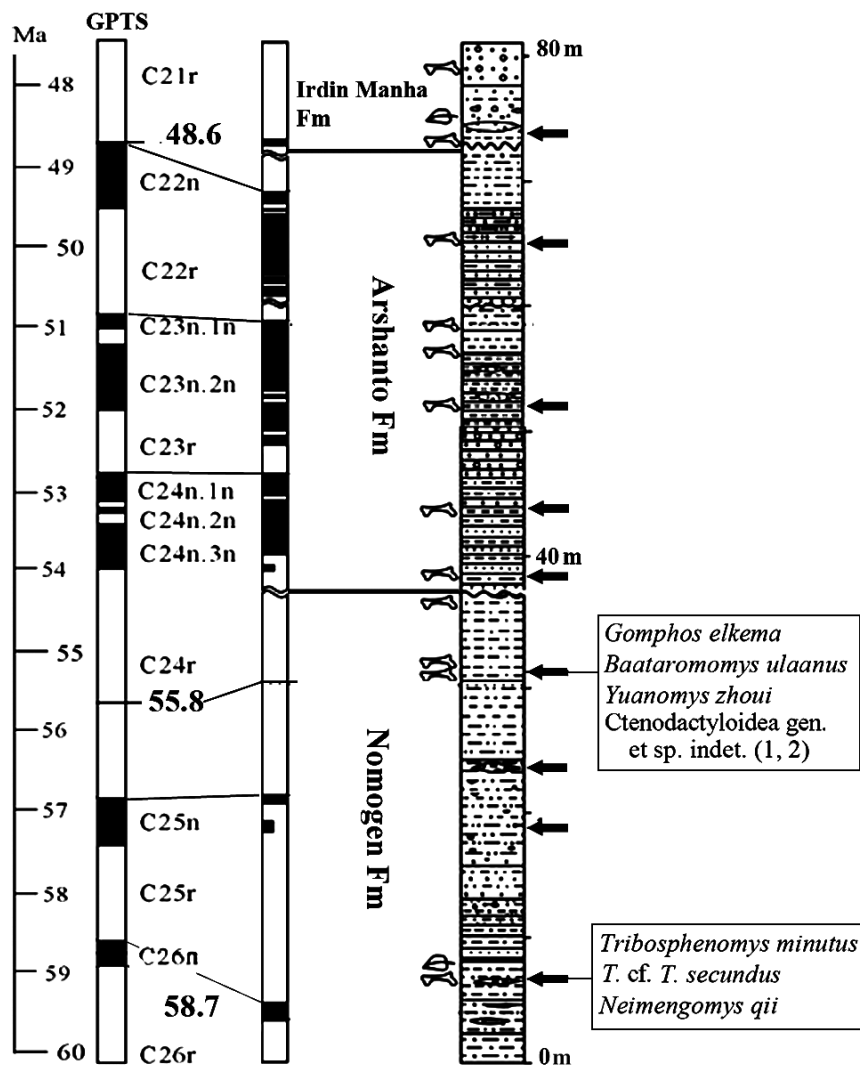


Fig. 1 A composed stratigraphic section showing occurrences of *Yuanomys zhoui* and related species. The diagram is modified from Meng et al. (2007c) and Sun et al. (2009); the arrows indicate beds where screenwashing samples were taken.

images have been edited using Adobe Photoshop CS4 version 11.0. Terminology for tooth structures follows Meng and Wyss (2001). IVPP is the Institutional abbreviation for the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing.

4 Systematic paleontology

Rodentia Bowdich, 1821

Ctenodactyloidea Simpson, 1945

***Yuanomys* gen. nov.**

Included species *Yuanomys zhoui*, type and only species.

Etymology *Yuan*, meaning “original” in Chinese.

Diagnosis Differs from alagomyids in having quadrate molars. Differs from other Early Eocene ctenodactyloid and paramyid rodents in having cuspsate cheek teeth in which the cusps and conules are distinctive, relatively slim and isolated. The paracone and metacone are transverse, instead of conical, and have steep surfaces facing the trigon basin. The trigon basin is a broad, transverse valley that distantly separates the paracone and metacone. The P4 protocone and paracone are conical and not inflated.

Yuanomys zhoui sp. nov.

Holotype IVPP V 16884, a fragmentary left maxilla with P4–M2 (Fig. 2A1–A5).

Included specimens IVPP V 16885, a right DP4 (Fig. 2B).

Etymology *Zhou*, in honor of Dr. Mingzhen Zhou.

Diagnosis Same as the genus.

Type locality and horizon Wulanboerhe, Erlian Basin, Nei Mongol (Inner Mongolia); upper part of the Nomogen Formation; earliest Eocene.

Description Tooth measurements (length/width in mm) are: V 16884, P4 (1.00/1.53), M1 (1.33/1.64), and M2 (1.40/1.67); V 16885, DP4 (17/1.47). The anterior surface of P4 does not bear a contact facet so that presence of a DP3 or P3 is unknown in this new specimen. A P3 is present in *Cocomys* (Li et al., 1989), *Bandaomys* (Tong and Dawson, 1995), *Tribosphenomys* (Meng et al., 1994; Meng and Wyss, 2001) and several specimens from the Bumban Member, Tsagan Khushu (Shevyreva, 1989; Dashzeveg, 1990a). We predict presence of the tooth in *Yuanomys*.

The molariform DP4 is assigned to the new species because of its matching size and general morphology. It is smaller and has a lower crown than M1. In occlusal view, the DP4 is roughly triangular with apexes rounded. The protocone is slightly larger than the metacone. Its anterior arm, the preprotocrista, extends anterolabially to meet the paraconule and continues in the same direction as the preparaconule crista toward the parastyle; it terminates before reaching to the latter. The paraconule is small and anterolingual to the paracone. The postparaconule crista is absent. Anterior to the preprotocrista is the precingulum that occurs anterior to the protocone and extends to the parastyle that is a ridge-like cusp forming the anterolabial corner of the tooth. The protocone connects the metaconule by a weak, if any, postprotocrista. The metaconule is distinct and connects the metacone by a low, curved premetaconule crista, which joins the anterolingual side of the metacone. Both paracone and metacone are conical and subequal in size. A weak postparacrista runs posterolabially to the labial edge of the tooth and ends as a tiny process that may be called the mesostyle. There is no centrocrista between the paracone and metacone. From the protocone a ridge extends posteriorly to a weak hypocone that is not quite cuspsate. The posterior margin of the tooth is formed by a low postcingulum.

P4 is nonmolariform and double-rooted. The cusp wear is shallower than that of M1, indicating that P4 erupted later than the molars. The P4 crown has two main cusps; the lingual one is homologized as the protocone and the labial one the paracone. Each cusp bears a steep wear facet on its anterior surface. The protocone and paracone are subequal in size. The shape of the protocone is somewhat similar to that of M1, extending anterolabially. However, the P4 protocone extends to join the midpoint of the precingulum, whereas the M1 protocone connects the paraconule. The precingulum is low but complete, extending from the anterior base of the protocone to the anterolabial corner of the tooth. A distinct conule posterolabial to the protocone is identified as the metaconule. Posterior to the protocone is a small but distinct hypocone, from which extends labially a short postcingulum. The relationship of these cusps and crests support the identification of the labial cusp as the paracone, instead of the metacone. The paracone is conical, and unlike the molars in which the labial surface of the paracone forms the labial border of the tooth, there is a narrow labial “cingulum” that forms the labial border of P4. This condition differs from the P4 in *Cocomys*, in which the P4

paracone forms the labial surface of the tooth. A small, triangular projection posterior to the paracone may be considered as an incipient metacone.

M1 is quadrate and triple-rooted with two labial small roots and one lingual major one. It is low crowned and has pronounced cusps and conules but weak crests. The protocone is teardrop shaped with the apex, the preprotocrista, extending anterolabially to join the paraconule. The worn tip of the cusp forms a concavity. The paraconule is distinct, which connects the paracone via a weak postparaconule crista. The preparaconule crista is absent. The paracone is almost an isolated cusp. It is transversely wide and anteroposteriorly short, with a steeper posterior surface. Its labial surface is rounded and forms the border of the tooth. The postparacrista is but the posterolabial edge of the cusp. The precingulum is prominent. It occurs anterior to the protocone and extends to the anterolabial corner of the tooth, where a parastyle is indistinct. The postprotocrista is weak. The metaconule is prominent and connects with the metacone via a weak premetaconule crista. The postmetaconule crista is absent. The metacone is also wider than long, but less so than the paracone. Its anterior surface is steeper than the posterior one. The premetacrista forms the anterolabial edge of the cusp. The trigon basin is a transverse and gently concave cleft. The centrocrista is absent. A weak mesostyle is oriented anteroposteriorly and blocks the labial exit of the trigon basin. The hypocone is posterior to the protocone; it is smaller and lower than the protocone. There is little connection between the two cusps. The postcingulum is narrow and runs from the hypocone to the posterolabial corner of the tooth.

The M2 is nearly identical to M1 in size and morphology.

Ctenodactyloidea gen. et sp. indet. 1

Included specimens IVPP V 16886, a left M2 (Fig. 2C).

Description This tooth measures 1.42 mm long and 1.62 mm wide, and is similar to M2 of *Yuanomys* in size. However, it bears some features that are different from the M2 of *Yuanomys*. This tooth seems less worn than the molars of *Yuanomys*, but it has a strong connection, the mure, between the protocone and hypocone. The protocone has two strong parallel arms: the anterior one ends at the paraconule anterolingual to the paracone and the posterior one extends labially to the lingual base of the paracone. Differing from *Yuanomys* the paracone and metacone of V 16886 are not so transverse, and nor so distantly separated. Moreover, the wear facet on the paracone or metacone is extensive and faces posterolingually. The wear facet of the paracone or metacone in *Yuanomys* is more parallel to the occlusal plane of the tooth. The metaconule of V 16886 is more inflated and confluent with the metacone, but the postprotocrista is absent between the protocone and metaconule. The mesostyle is more developed and transversely oriented. The trigon basin is narrow. Because of these differences, we hesitate to assign it to *Yuanomys*. Although some features of the tooth also differ from those of Bumban specimens, we have less confidence about these differences. The taxonomic position of this tooth needs to be clarified when more specimens become available.

Ctenodactyloidea gen. et sp. indet. 2

Included specimens IVPP V 16887, a left M2 (Fig. 2D).

Description This is a distinctively larger specimen (2.15 mm long, 2.28 mm wide) that does not match any of the rodents known from the same locality. Because of its narrower posterior half of the tooth, this isolated tooth is most likely a M2. This tooth bears little wear. The precingulum is well developed with its lingual end inflated as a cusplule and labial end joining a distinct parastyle. The protocone is relatively anterior to be at the lingual side of the paracone so that it is distantly separated from the hypocone; both cusps are connected by a long, curved mure. Similar to V 16886, there are two arms derived from the protocone. The anterior one, the preprotocrista, is stronger and joins the paraconule labially. The posterior arm is short and

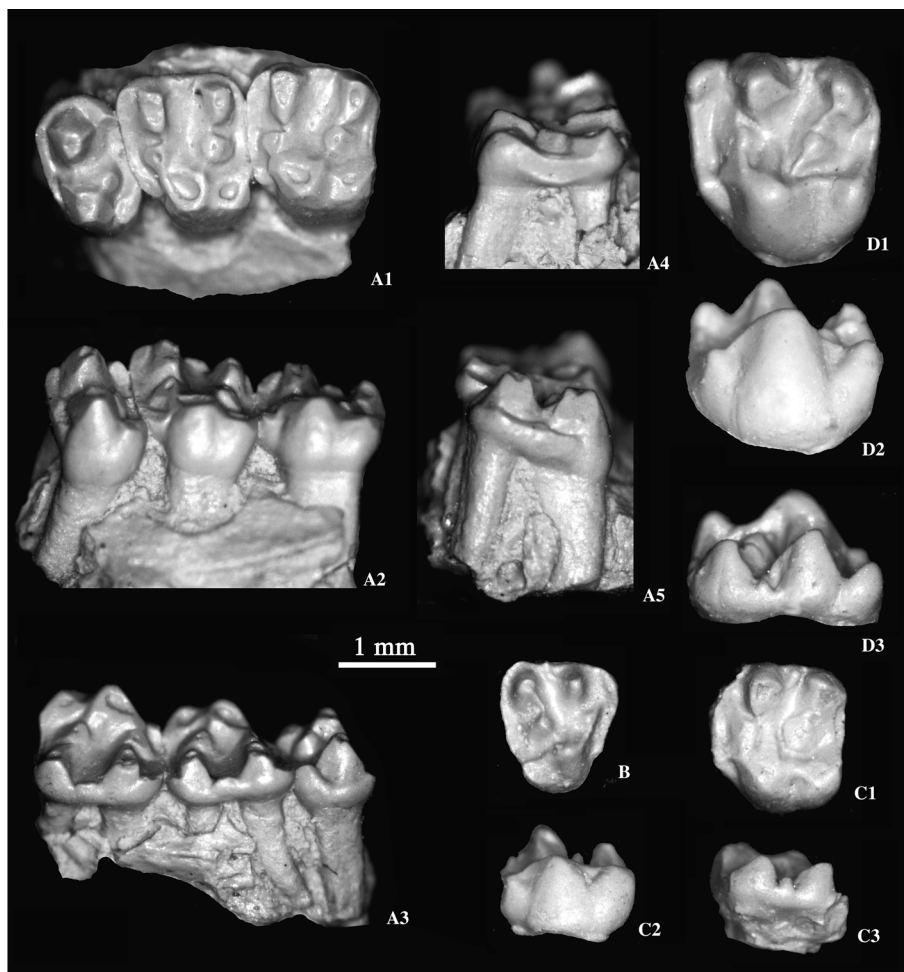


Fig. 2 Teeth of Early Eocene rodents from the Erlian Basin, Nei Mongol

A1–A5. occlusal, lingual, buccal, posterior and anterior views of P4–M2 of *Yuanomys zhoui* (IVPP V 16884, holotype); B. occlusal view of DP4 of *Yuanomys zhoui* (IVPP V 16885); C1–C3. occlusal, lingual and buccal views of M2 of the small *Ctenodactyloidea* gen. et sp. indet. (IVPP V 16886); D1–D3. occlusal, lingual and buccal views of M2 of the large *Ctenodactyloidea* gen. et sp. indet. (IVPP V 16887); all are on the same scale

low, fading away before reaching to the base of the paracone. The preparaconule crista is low and joins the anterolingual side of the paracone. The paracone is isolated and larger than the metacone. The metaconule is distinct and connects the protocone with a narrow postprotocrista lingually and the metacone with a premetaconule crista. The hypocone is well developed and continues with the posteingulum that extends to the posterior side of the metacone. This tooth probably represents a different species from *Yuanomys zhoui* because of its larger size and different morphology. It also differs from all Bumban specimens, as we can compare from the published figures and descriptions.

5 Comparison

With ctenodactyloid rodents We compare the new species only with the earliest cteno-

dactyloid rodents known from Asia, including *Cocomys lingchaensis* (Li et al., 1989), *Bandaomys zhonghuaensis* (Tong and Dawson, 1995) and taxa reported from the Bumban Member of Naran-Bulak Formation, Tsagan Khushu, Mongolia (Shevyreva, 1989; Dashzeveg, 1990a). Other later forms, such as those reviewed by Averianov (1996), are apparently more advanced than the new species and will not be compared.

Based on its cranial and dental morphologies *Cocomys lingchaensis* has been considered as the representative of most primitive rodents and has often been placed at the basal position of the clade of Rodentia (Meng et al., 2003; Asher et al., 2006). *Cocomys* (Fig. 3A–C), however, is distinctively different from the new species. *Cocomys* is larger (see Li et al., 1989; table 1). Its DP4 hypocone is isolated and the preparacone crista connecting to the paracone rather than extending toward the parastyle, and all cusps are more inflated so that cusps and conules are less isolated. On P4, *Yuanomys* differs from *Cocomys* in having a distinct metacone and hypocone; the protocone and paracone in *Yuanomys* are proportionally smaller and more conical. In addition, *Cocomys* has a weak, if any, labial cingulum. The molars of *Cocomys* have more inflated and conical cusps with rounded surface, development of a weak centrocrista, and a larger mesostyle.

The holotype of *Bandaomys zhonghuaensis* also preserves P4–M2. Its P4 has more inflated protocone and paracone and a rudimentary metacone. The cusps and conules of molars in *Bandaomys* are more inflated and more closely connected by crests than in *Yuanomys*.

The comparison with rodents from the Bumban Member, Tsagan Khushu, Mongolia proves to be difficult because we have no access to the original specimens and because the Bumban species were inadequately known, as pointed out by Tong and Dawson (1995). Tong and Dawson (1995:56) noted that the Bumban rodents were under revision by J. –L. Hartenberger, but the revision has not been published to our knowledge. Tong and Dawson cautioned the difficulty to establish any new taxon when some of the Bumban rodents remain uncertain in their morphologies and taxonomic positions. Averianov (1996) presented a review on Eocene rodents known at the time. For rodents from the Bumban member, Averianov considered *Tsagankhushumys deriphatus* as a valid taxon (= *T. onos*; = *Bumbanomys edestus*; = *Sharomys singularis*; = *S. parvus*; = *Kharomys mirandus*; = *Ulanomys mirificus*). Averianov omitted *Kharomys gracilis* and *Tsagamys subitus* in the list of synonyms. Judging from wording in the context, such as “we accept here only one species of small tamquammyid for the Tsagan Khushu locality” (Averianov, 1996:636), we assume that these two species should be included in the list as well. Averianov considered *Euboromys grandis* (Dashzeveg and McKenna, 1991; = *Boromys* Dashzeveg, 1990a) as a valid taxon from Tsagan Khushu and placed it in the list of rodents from that locality (Averianov, 1996; table 2). However this rather large species actually came from a different locality: Khaichin-Ula II of Khaichin Formation, Middle Eocene (Dashzeveg, 1990a). Averianov recognized *Adolomys*, *Esesempomys* and *Orogomys* from Tsagan Khushu as valid taxa, but he considered *Orogomys* as a tamquammyid rodent instead of an alagomyid, as Dashzeveg (1990b) originally identified.

In a personal note to Dr. M. Dawson, which became available to us as a courtesy from Dr. Dawson, J. –L. Hartenberger made the following observations when he examined the specimens under the care of Shevyreva in Moscow: *Tsagankhushumys deriphatus* (= *Tsagamys subitus*) is a valid taxon and *Sharomys singularis* is a valid species but is also considered as a possible synonym of *Tsagankhushumys onos*. This uncertainty perhaps stems from the fact that the type specimen of *T. onos* was not available to Hartenberger at the time. *Adolomys ameristus* (= *Sharomys parvus*) is a valid taxon. *Bumbanomys edestus* (= *Kharomys mirandus* + *K. gracilis* + *Ulanomys mirificus*) is a valid species. The type specimen of *Esesempomys centralasize* was unavailable at the time. *Orogomys obscurus* was considered a synonym of *Ivanantonia efremovi*. For those species whose type specimens are not available, Hartenberger considered them as *nomina nuda*.

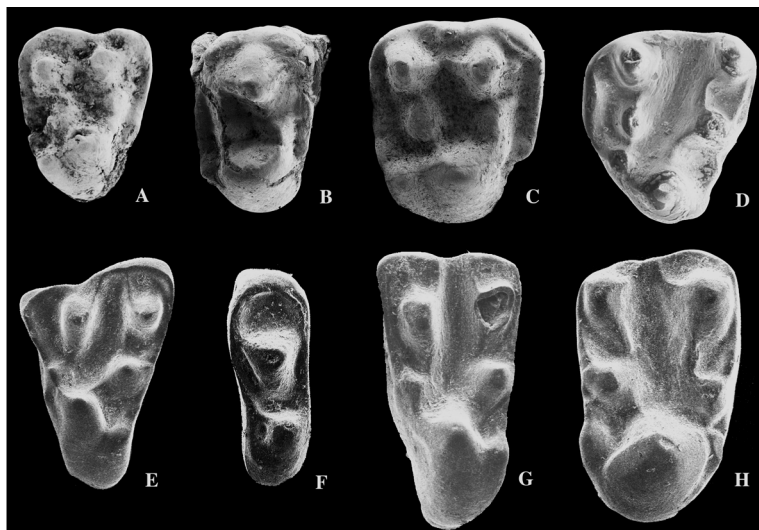


Fig. 3 Occlusal views of teeth for comparison

A–C. DP4, P4 and M1 of *Cocomys lingchaensis*; D. M1 of *Archetypomys erlianensis* (from Meng et al., 2007a); E–G. DP4, P4 and M1 of *Tribosphenomys minutus* (from Meng et al., 2007b); H. M2 (or M1) of *Neimengomys qii* (from Meng et al., 2007b); the images are not on the same scale

Apparently, the taxonomy of rodents from the Bumban Member, Tsagan Khushu, is more complex than we can possibly sort out, and we do not anticipate any substantial revision of those rodents in near future. In this study, instead of comparing *Yuanomys zhoui* with each of the named Bumban species, we make a general comparison with the upper teeth of rodents from Bumban Member that have been described, discussed, and at least in some way, illustrated. Our comparison shows that, although all of the specimens assigned to Ctenodactyloidea have the typical ctenodactyloid tooth pattern, none of the specimens from the Bumban Member, Tsagan Khushu, has the kind of cusps dental morphology of *Yuanomys zhoui*. All upper molars known from Bumban have more inflated cusps and conules, and none of them show transversely wide but anteroposteriorly short paracone and metacone separated by a broad trigon valley. All of them are generally larger than *Yuanomys zhoui*. Because of these differences, we think the proposal of *Yuanomys zhoui* is justified.

With paramyids Earliest paramyids in Asia are known from the Lower Eocene, Wutu, Shangdong, China (Tong and Dawson, 1995). Two species, *Taishanomys changlensis* and *Acritoparamys? wutui*, are based exclusively on lower dentitions, making further comparison difficult. Nonetheless, the sizes of the Wutu species as reflected by their lower teeth are significantly larger than that of *Yuanomys*.

The earliest rodent, a paramyid, is *Paramys adamus* from the early Clarkforkian (Cf1), Big Multi Quarry, Washakie Basin, Wyoming (Dawson and Beard, 1996). *P. adamus* is larger than *Yuanomys*; its P4 has well developed paracone and metacone. As in other early rodents, the cusps and conules are more inflated and the trigon valley is more restricted than those of *Yuanomys*.

With alagomyids As discussed by Meng et al. (2007a), the primary difference between the tooth patterns of alagomyids and rodents is the narrowing of the cheek teeth in rodents. From *Tribosphenomys* to more advanced rodents, M1 changes from being wider transversely to being longer anteroposteriorly. Meng et al. (2007a) considered that the quadrate tooth of rodents is achieved by narrowing the tooth instead of increasing its anteroposterior length and that the difference in tooth dimensions probably reflects a functional transition in mastication.

tion, in which the transverse component of the masticatory stroke may have been reduced in rodents compared to alagomyids. However, Meng et al. (2007a) focused on *Archetypomys erlianensis*, which is geologically younger than the new rodent reported here and morphologically unique in Eocene rodents. Because the most speciose groups among the earliest rodents of modern aspect are the ctenodactylids in Asia and the paramyines in North America, to which the cheek teeth of *Yuanomys* are generally more comparable, a further comparison of dental morphology between *Yuanomys* and alagomyids may cast new light on the transformation of rodent tooth.

Unlike other basal Glires, those that are commonly called eurymylids and mimotonids, the cheek teeth of alagomyids are more comparable to the general tribosphenic tooth pattern in having a low tooth crown with distinct cusps but weak crests. Nearly all dental cusps, conules and crests can be homologized with those of a typical tribosphenic molar of therian mammals (Meng and Wyss, 2001), which narrows the morphological gap between the typical tribosphenic tooth pattern and the typical rodent molar.

The DP4 of *Yuanomys* differs from that of *Tribosphenomys* (Fig. 3E) in being transversely narrower, resulted from a combination of loss of the labial shelf, addition of the precingulum, the base of the protocone being more labially retracted, a more developed hypocone and postcingulum. The arrangement of the cusps remains similar. On the DP4 of *Tribosphenomys*, there is a sign of the precingulum. The P4 of *Yuanomys* differs from that of *Tribosphenomys* (Fig. 3F) in having the labial shelf reduced, tooth length proportionally increased, development of the metaconule and hypocone. The P4 paracone of *Yuanomys* remains conical, somewhat similar to the P4 central cusp of *Tribosphenomys*. This lends some support to the notion that the labial cusp in *Tribosphenomys* is the paracone.

Among Early Eocene rodents, the molar cusp morphology of *Yuanomys* is best comparable to that of alagomyids, including *Alagomys* (Dashzeveg, 1990b; Tong and Dawson, 1995; Dawson and Beard, 1996), *Tribosphenomys* (Meng et al., 1994, 2007b; Meng and Wyss, 2001; Dashzeveg, 2003; Lopatin and Averianov, 2004a,b; Fig. 3G) and *Neimengomys* (Meng et al., 2007b; Fig. 3H). In general, the tooth cusps and conules in *Yuanomys* and alagomyids are pronounced and crests are weak. The paracone and metacone are transverse with a steep surface facing the trigon basin. The paracone and metacone are distantly separated by a broad trigon valley that extends transversely.

Compared to molars of *Tribosphenomys* (Fig. 3G) and *Neimengomys* (Fig. 3H), the molar of *Yuanomys* is quadrate, which is resulted from reduction of the labial shelf, labial retraction of the protocone base, development of the precingulum, expansion of the hypocone, and development of the postcingulum that is separated from the metaconule. The development of the mesostyle is also a feature common for *Yuanomys* and other rodents. The molar of *Neimengomys* is more similar to that of *Yuanomys* in having the following features; the tooth is proportionally less transverse; the labial shelf is narrowed; a rudimentary precingulum is developed anterior to the protocone; the hypocone is more developed.

With cylindrodontid *Tuscahomys* *Tuscahomys* is considered the oldest and most primitive cylindrodontid rodents. The genus is based on isolated teeth from the earliest Wasatchian estuarine deposits at the Red Hot Truck Stop locality in the T4 sand, Tuscahoma Formation, near Meridian, Mississippi (Dawson and Beard, 2007). In addition to alagomyids and paramyids, *Tuscahomys* represents another group of earliest Glires from North America, which indicates a more diverse rodent fauna in the Early Eocene of North America than previously known.

A total of four species have been assigned to the genus and all are larger than *Yuanomys* (Dawson and Beard, 2007; table 1). The P4 of *Tuscahomys* is similar to that of early Paramyidae in having the paracone and metacone close together. However, *Tuscahomys* are distinctive in having the following combination of derived upper tooth characters; moderate lingual hypso-

donty of upper cheek teeth; anteroposterior lingual ridge, or mure, formed of elongated protocone and distinct hypocone area; relatively slight indication of lingual groove between protocone and hypocone (Dawson and Beard, 2007:141). All these features distinguish *Tuscahomys* from *Yuanomys*. The cheek teeth of *Tuscahomys* is transversely wider than those of *Yuanomys*. This is probably resulted from the moderate lingual hypsodonty of the upper cheek teeth of *Tuscahomys*, instead of retention of the primitive condition in basal Glires, such as alagomyids.

With *Archetypomys* *Archetypomys* is a unique rodent from a stratum slightly younger than *Gomphos* bed in the same region (Meng et al., 2007a,c). It has some dental features similar to those of alagomyids, such as a weak buccal cingulum, a distinct metaconule that merges posteriorly with the postcingulum, a transversely oriented trigon basin that widely separates the paracone and metacone, and absence of the hypocone (Meng et al., 2007a; Fig. 3D). *Archetypomys* has a preprotoconule, a unique feature unknown in other early rodents. In addition, it lacks a true precingulum. *Yuanomys* is similar to *Archetypomys* in having a transversely narrowed tooth crown with a broad trigon valley, but differs from the latter in having some more typical dental features of early rodents, such as development of the precingulum, presence of the hypocone, and a postcingulum that is separated from the metaconule. In addition, the paracone and metacone of *Yuanomys* are more transverse and bear steep surfaces facing the trigon basin, as in alagomyids. In contrast, the paracone and metacone of *Archetypomys* are more conical.

6 Divergence of rodents

The comparison above indicates that, if alagomyids represent the outgroup morphotype for rodents (Meng et al., 2003; Asher et al., 2005), *Yuanomys* displays more primitive dental features similar to alagomyids than cocomyids and paramyids. This raises the issue about the divergence of early rodents. It has been widely accepted that rodents probably originated from Asia because nearly all sister taxa of rodents occurred in the Paleocene of Asia and because the Early Eocene rodents of Asia are diverse (Li et al., 1979; Dashzeveg and Russell, 1988; Meng, 2004; Meng and Wyss, 2001; Meng et al., 2003; Asher et al., 2005). In contrast, only one species of alagomyids, *Alagomys russelli*, is known from the early Clarkforkian (Cf1), Big Multi Quarry, Washakie Basin, Wyoming, North America (Dawson and Beard, 1996). Interestingly, the earliest known rodent with modern aspect, *Acritoparamys*, coexists at the same locality with *Alagomys russelli*. According to the geological time scale of the Paleogene (Luterbacher et al., 2004), the age of the North American *Acritoparamys*, that is, the early Clarkforkian (Cf1), is slightly younger than 57 Ma. The age of the earliest rodents in Asia is the earliest Eocene Bumbanian, no older than 55.8 Ma (Luterbacher et al., 2004). Then, there is a 1 Ma difference between the oldest fossil records of rodents with modern aspect in North America and Asia, which seems contradicting the scenario that Asia is the origin center of rodents.

However, the age determination of the Asian land mammal ages, such as the Bumbanian, is mainly based on biostratigraphic correlation and is by no means accurate. It has been argued that the Bumbanian is not Early Eocene, but Late Paleocene, correlative to part of the Clarkforkian (Beard, 1998). The primitive nature of *Yuanomys* in comparison with *Acritoparamys* lends support to Beard's view. A recent magnetostratigraphic work places the *Gomphos* bed near the Paleocene–Eocene boundary within the long C24r (Sun et al., 2009). However, because of a sedimentary hiatus that truncated the upper Nomogen Formation in the sequence, the possibility cannot be excluded that the *Gomphos* bed is actually older. In the same study (Sun et al., 2009) the Gashatan fauna containing *Tribosphenomys* and *Neimengomys* is considered the earliest Late Paleocene, with an age slightly older than 58 Ma; this is therefore correlative to mid-Tiffanian (Ti3). If this age determination is correct, the Gashatan fauna containing *Tribosphe-*

nomys and *Neimengomys* in Asia is at least 1 Ma older than the Big Multi Quarry that produces *Alagomys russelli* and *Acritoparamys*. This age difference is consistent with the morphological evolution between *Tribosphenomys*–*Neimengomys* and *Alagomys russelli*.

In our working area in Erlian Basin screenwashing of matrices from strata between the lower Nomogen Fm. containing the Gashatan fauna and the upper Nomogene Fm. containing *Gomphos* and *Yuanomys* have generated fragmentary fossils (Fig. 1). Considerable effort of screenwashing has also been carried out in various localities in Asia, but no rodent with modern aspect has been discovered from strata between the Gashatan and Bumbanian sediments. Immediately above the *Gomphos* bed, a truly radiation of rodents took place around 54 Ma, where, in addition to several kinds of ctenodactyloids, mydonts and *Archetypomys* made their first appearances. The fossil record demonstrates again that Asia is probably the origin center of rodents and that the earliest divergence of rodents probably took place during the period of time from the mid-Paleocene to the earliest Eocene. The discoveries of the earliest Wasatchian cylindrodontids from North America and additional species from the Bumbanian fauna of Asia indicate that the early diversity of rodents is higher than what we understood previously and that after their divergence as a morphologically distinctive group, rodents have evolved separately in Asia and North America.

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References

- Asher R J, Meng J, McKenna M C et al., 2005. Stem lagomorpha and the antiquity of Glires. *Science*, **307**: 1091–1094
- Averianov A, 1996. Early Eocene Rodentia of Kyrgyzstan. *Bull Mus Natl Hist Nat, Paris*, **18**: 629–662
- Beard K C, 1998. East of Eden; Asia as an important center of taxonomic origination in mammalian evolution. Special Volume of the Symposium on Cretaceous and Early Tertiary Mammals of Asia. *Bull Carnegie Mus Nat Hist*, **34**: 5–39
- Bowen G J, Koch P L, Meng J et al., 2005. Age and correlation of fossiliferous late Paleocene-early Eocene strata of the Erlian Basin, Inner Mongolia, China. *Am Mus Novit*, (3474): 1–26
- Dashzeveg D, 1990a. The earliest rodents (Rodentia, Ctenodactyloidea) of Central Asia. *Acta Zool Cracov*, **33**: 11–35
- Dashzeveg D, 1990b. New trends in adaptive radiation of early Tertiary rodents (Rodentia, Mammalia). *Acta Zool Cracov*, **33**: 37–44
- Dashzeveg D, 2003. A new species of *Tribosphenomys* (Glires, Rodentia) from the Early Eocene of Nemegt Basin, Mongolia and its implication for alagomyid phylogeny. *Proc Mongol Acad Sci*, (1): 49–62
- Dashzeveg D, McKenna M C, 1991. *Euboromys*, a new name for the Eocene rodent *Boromys* Dashzeveg, 1990, not *Boromys* Miller, 1916. *J Vert Paleont*, **11**(4): 527
- Dashzeveg D, Russell D E, 1988. Palaeocene and Eocene Mixodontia (Mammalia, Glires) of Mongolia and China. *Palaeontology*, **31**: 129–164
- Dawson M R, Beard C K, 1996. New Late Paleocene rodents (Mammalia) from Big Multi Quarry, Washakie Basin, Wyoming. *Palaeovertebrata*, **25**: 301–321
- Dawson M R, Beard C K, 2007. Rodents of the family Cylindrodontidae (Mammalia) from the earliest Eocene of the Tuscahoma Formation, Mississippi. *Ann Carnegie Mus*, **76**: 135–144
- Dawson M R, Li C K, Qi T, 1984. Eocene ctenodactyloid rodents (Mammalia) of eastern central Asia. *Carnegie Mus Nat Hist Spec Publ*, **9**: 138–150

- Li C K., Chiu C S., Yan D F et al., 1979. Notes on some Early Eocene mammalian fossils of Hengdung, Hunan. *Vert Palasiat*, **17**(1): 71–80 (in Chinese with English abstract)
- Li C K., Zheng J J., Ting S Y., 1989. The skull of *Cocomys lingchaensis*, an Early Eocene Ctenodactyloid rodent of Asia. In: Black C C., Dawson M R eds. *Papers on Fossil Rodents in Honor of Albert Elmer Wood*. *Nat Hist Mus Los Angeles County Sci Ser*, **33**: 179–192
- Lopatin A V., Averianov A O., 2004a. A new species of *Tribosphenomys* (Mammalia: Rodentiaformes) from the Paleocene of Mongolia. In: Lucas S G., Zeigler K E., Kondrashov P E eds. *Paleogene Mammals*. *New Mexico Mus Nat Hist Sci Bull*, **26**: 169–175
- Lopatin A V., Averianov A O., 2004b. The earliest rodents of the genus *Tribosphenomys* from the Paleocene of Central Asia. *Dokl Biol Sci*, **397**: 336–337
- Luterbacher H P., Ali J R., Brinkhuis H et al., 2004. The Paleogene Period. In: Gradstein F., Ogg J., Smith A eds. *A Geological Time Scale 2004*. Cambridge: Cambridge University Press. 384–408
- Meng J., 2004. Phylogeny and divergence of basal Glires. *Bull Am Mus Nat Hist*, **285**: 93–109
- Meng J., Bowen G J., Ye J et al., 2004. *Gomphos elkema* (Glires, Mammalia) from the Erlian Basin: evidence for the Early Tertiary Bumbanian Land Mammal Age in Nei-Mongol, China. *Am Mus Novit*, (3425): 1–24
- Meng J., Hu Y M., Li C K., 2003. The osteology of *Rhombomylus* (Mammalia, Glires): implications for phylogeny and evolution of Glires. *Bull Am Mus Nat Hist*, **275**: 1–247
- Meng J., Li C K., Wang Y Q et al., 2007a. A new Eocene rodent from the lower Arshanto Formation in the Nuhetingboerhe (Camp Margetts) area, Inner Mongolia. *Am Mus Novit*, (3569): 1–18
- Meng J., Ni X J., Li C K et al., 2007b. New material of Alagomyidae (Mammalia, Glires) from the Late Paleocene Subeng locality, Inner Mongolia. *Am Mus Novit*, (3597): 1–29
- Meng J., Wang Y Q., Ni X J et al., 2007c. New stratigraphic data from the Erlian Basin: definitions, divisions and correlations of Paleogene stratigraphic units in Inner Mongolia. *Am Mus Novit*, (3570): 1–31
- Meng J., Wyss A R., 2001. The morphology of *Tribosphenomys* (Rodentiaformes, Mammalia): phylogenetic implications for basal Glires. *J Mammal Evol*, **8**(1): 1–71
- Meng J., Wyss A R., Dawson M R et al., 1994. Primitive fossil rodent from Inner Mongolia and its implications for mammalian phylogeny. *Nature*, **370**: 134–136
- Meng J., Zhai R J., Wyss A R., 1998. The Late Paleocene Bayan Ulan fauna of Inner Mongolia, China. In: Beard K C., Dawson M R eds. *Dawn of the Age of Mammals in Asia*. *Bull Carnegie Mus Nat Hist*, **34**: 148–185
- Ni X J., Beard K C., Meng J et al., 2007. Discovery of the first early Cenozoic euprimate (Mammalia) from Inner Mongolia. *Am Mus Novit*, (3571): 1–11
- Shevyreva N S., 1989. New rodents (Ctenodactyloidea, Rodentia, Mammalia) from the Lower Eocene of Mongolia. *J Palaeont*, **3**: 60–72 (in Russian)
- Sun B., Yue L P., Wang Y Q et al., 2009. Magnetostratigraphy of the early Paleogene in the Erlian Basin. *J Stratigr*, **33**: 62–68 (in Chinese with English summary)
- Tong Y S., Dawson M R., 1995. Early Eocene rodents (Mammalia) from Shangdong Province, China. *Ann Carnegie Mus*, **64**: 51–63
- Wang Y Q., Meng J., Ni X J et al., 2008. A new Early Eocene arctostylopoid (Arctostylopida, Mammalia) from Erlian Basin, Nei Mongol (Inner Mongolia), China. *J Vert Paleont*, **28**(2): 553–558